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浑善达克沙地不同植物功能型光合作用和水分利用特征的比较

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摘要:为了比较不同植物功能型在沙地生境下光合作用和水分利用效率的差异,测定了浑善达克沙地 3 种功能型的代表种的气体交换特征来比较它们的光合碳固定能力和水分利用状况。3 个代表种的气体交换日变化结果表明乔木的光合速率和水分利用效率比草本和灌木的低,而蒸腾速率和气孔导度较高,经过中午的光合午休后,乔木的光合速率在下午没有恢复,而草本和灌木都有不同程度的恢复。在所测定的所有代表物种中,研究地全部的乔木(3 种)和灌木(6 种)以及典型的草本(25 种),气孔导度与光合速率和蒸腾速率都成显著的正相关关系;另外,在同样的叶片水势情况下,乔木植物的气孔导度最低,在同样的蒸腾速率情况下,乔木植物的光合速率最低。这些结果表明乔木在 CO_2 同化和 H_2O 蒸腾平衡上具有低的水分利用效率。从这个角度考虑,我们认为在对沙地进行恢复时,一些草本和灌木种比乔木更合适。

关键词:浑善达克沙地;气体交换;植物功能型;气孔调节;水分利用效率

Comparison of photosynthesis and water use efficiency between three plant functional types in Hunshandak sandland

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Abstract: Stomata controls carbon-water balance in plants by acting as transport for diffusive CO_2 uptake and water vapor loss. Plants with lower photosynthesis and higher transpiration rate may function with less stomatal control and inefficient water usage. To test the hypothesis that tree is improper for the purpose of degraded land restoration in arid or semi-arid environment, we investigated gas exchanges of three plant functional types (PFTs) (3 tree species, 6 shrub species and 25 herb species) in Hunshandak Sandland, China, to compare their carbon assimilation ability and water use efficiency. Our research aimed to look into how those plants with different PFTs design carbon and water cycling in semi-arid areas in order to select the ecologically and economically suitable species for the seek of controlling of sandland degradation.

We investigated the typical species of each PFT, i.e. *Ulmus pumila* (tree), *Salix gordejevii* (shrub) and *Leymus chinensis* (herb) to compare their diurnal gas exchange changes. The results showed that trees had significantly lower photosynthetic rates (A) and water use efficiency (WUE), but higher transpiration rate (E) and stomatal conductance (g_s), compared with herbs and shrubs. Tree species decreased their A, E and g_s all along from the maximal values in the morning and could not recover in the afternoon, while shrubs and herbs reopened their g_s after the midday depression. The diurnal changes of g_s indicated the less stomatal flexibility of stomata in trees than herbs and shrubs.

Furthermore, all the trees (3 species), shrubs (6 species) and the dominant herbs (25 species) were compared for the stomatal control and water use efficiency among PFTs. Among all the species with different PFTs, there were significantly positive correlations between g_s and A and E. However, tree species displayed lower A but higher E than shrubs and herbs at the same stomatal conductance, indicating that tree species assimilate less CO_2 and transpire more water per unit g_s. Lower photosynthetic capacity and larger transpiration rate induced less water use efficiency in trees than in shrubs and herbs. In

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addition, g_s in trees were more possible to suffer from the drought as reflected by the sensitivity of g_s to varied leaf water potential. These results might suggest that trees had poor stomatal regulation in controlling carbon-water balance and more sensitive to drought which was common in Hunshandak Sandland. From this study, we recommend that some native herbs, such as *Leymus chinensis* and *Agriophyllum squarrosum* and shrubs, like *Salix matsudana* Koidz, *Salix gordejevii* L., rather than trees should be selected for the sandland restoration.

Key words: Hunshandak sandland; gas exchange; plant functional types; stomatal regulation; water use efficiency

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Introduction

Drought is the key factor limiting plant growth in arid and semi-arid environments[1]. Plants respond to water shortage by different ecological strategies, as reflected by their related eco-physiological characteristics[2,3]. Efficient water use has been proposed either to increase plant biomass production or support drought tolerance[4]. Those with such character always have the special eco-physiological or structural traits to avoid danger of dryness, *i.e.*, deeper root system for a greater water uptake[5,6]、an ability to reduce leaf transpiration rates[7], adjustment to leaf water potential[8] and sensitive stomatal control of water losses[9,10]. Of all the traits, stomatal control and efficient water utilization are especially important, because a favorite H_2O balance in leaf tissues while acquiring CO_2 is the primary function in plants responding to water stress[11,12]. Recently, the study of the physical and biochemical processes related to water drought stress has offered an opportunity in advancing a more general understanding of drought resistance in different plant functional types (PFTs)[13].

Plant functional types (PFTs) means a group of plant species that share similar traits, morphological or physiological in an ecosystem[14,15]. Such term provides a logical link between physiological and life-history strategies at both individual and ecosystem levels[16]. The characteristics of photosynthesis in different PFTs[17] related to different environmental factors[18] were analyzed along a transect in North China. However, the PFTs composed of trees, shrubs and herbs growing in the similar habitats were poorly understood from points of the ecophysiological and their co-existence strategies.

Hunshandak sandland is one of the most degraded grassland in China, which is recently blamed as the source of sand dust storms[19]. Overgrazing is regarded as the most important cause of desertification there[20]. Vegetation restoration is considered as one of effective ways to combat desertification and prevent adjacent areas from sand encroachment in many of the deserted regions of the world[21]. However, what species we should select is a controversial topic in this field. Although some people persist that trees in Hunshandake Sandland act as an efficient ecological barrier to sand dust storm, more and more ecologists argue that it is impossible for the planted trees to develop into forestry in regions which receive precipitations less than 400 mm/a[22~24]. One of the primary factors that limit land restoration is water shortage, becoming the main driving force in shaping different functional vegetation compositions in the arid or semiarid systems[25,1]. Water use strategy of PFTs (e.g. grasses, shrubs and trees) must be fully understood before tree or shrub planting activities being executed. Therefore, the study on ecophysiological response to arid environment from different PFTs's could help the decision makers to wisely choose the suitable species before land restorations being conducted.

Our research aimed to look into how those plants with different PFTs design carbon and water cycling in arid areas. Thereafter, based on which, some ecologically and economically suitable species should be brought forward for the seek of controlling of degradation.

1 Materials and methods

1.1 Study area The investigation was conducted at Hunshandak Sandy Ecosystem Research Station of the Chinese Academy of Sciences (42°23′N, 112°23′ E), which is located in the middle of Xilingel League of Inner Mongolia Autonomous Region of China. The climate is of cold-temperate arid and semi-arid. The average annual temperature is about 1.7℃, with the monthly maximum (July) and minimum (January) being 16.6℃ and −24.1℃, respectively. The annual accumulative temperature of above 10℃ is 2600℃. The frostless period is approximately 100 days. This area receives annual precipitation about 250～350mm, with uneven distribution throughout the years. The maximum values (30 mm/month) was observed from June to August and the minimum values (3 mm/month) from March to May. The annual potential evaporation is about 2000～2700mm.

1.2 Plants According to our field investigation, there are 3 tree species, 6 shrub species and some 600 herbaceous species in the study area. Three-year enclosed grassland was selected as the experiment site, which had vegetation cover of 60%. Trees and shrubs sparsely distributed, occupying 20%~30% of the whole vegetation cover. We surveyed all the trees (3 species), shrubs (6 species) and the dominant herbs (25 species) to compare their stomatal control and water use efficiency. PFTs were classified according to their life forms. Trees species are composed of *Ulmus pumila*, *Malus baccata* and *Salix matsudana*. Shrubs are *Salix gordejevii*, *Caragana microphylla*, *Lonicera chrysantha*, *Betula fruticosa*, *Ribes pulchellum* and *Amorpha fruticosa*. For herbs, *Corispermum heptapotamicum*, *Salsola collina*, *Leymus chinensis*, *Agriophyllum squarrosum*, *Astragalus efoliolatus*, *Saussurea runcinata*, *Chenopodium glaucum*, *Artemisia ordosica*, *Ferula bungeana et al.* are commonly found. Of all the species, *U. pumila* took about 90% of trees, *Salix gordejevii* 50% of shrubs and *Leymus chinensis* 30% of grasses. In July of 2001, all the 34 mentioned species were measured with gas exchange and water potentials. On 5 and 6 July, 2002, one representative species of each PFT, i.e. *Ulmus pumila* for tree, *Salix gordejevii* for shrub and *Leymus chinensis* for grass was chosen to compare their diurnal gas exchange.

1.3 Gas exchange measurements Leaf gas exchange was measured by a portable photosynthesis system (LCA-4, ADC, Hoddesdon, England). In July of 2001, 3 plants per species were measured from 8:00 when photosynthetic photon flux density (PPFD) was above light saturated point and stopped at 11:00 (to avoid high radiation stress) on all clear days. The maximal photosynthetic rate appeared during this time period[26]. When taking measurement, the fully-expanded functional leaves in upper shoots were selected. Parameters determined were carbon assimilation (A), transpiration rate (E) and stomatal conductance (g_s). Leaf areas for calculation of gas exchange were measured by an Area Meter (AM100, ADC, Hoddesdon, England). Water use efficiency (WUE) was calculated by A/E.

Diurnal gas exchange of the three representative species was measured on 5 and 6 July, 2002 from 6:00 to 20:00 at two-hours intervals.

1.4 Leaf water potential After gas exchange measurement, fully expanded leaves with little twigs were taken around the tops of plants as the leaf samples. Leaf water potential (Ψ_{leaf}) was measured by using WP4 Dewpoint Potential Meter (Decagon Devices, Inc., Pullman Washington, USA). The detailed method for leaf water potential measurement has been reported by the same research team[23].

1.5 Data analysis Data for each of the three PFTs were pooled in order to assess the correlations amongst physiological variables. The ultimate gas exchange data of each species was the mean of three plants. Data were analyzed using ANOVA followed by a least significance difference test (LSD) with $p<0.05$. Tukey's Studentized Range Test was used to identify significant differences between PFTs ($p<0.05$). Correlation coefficients were calculated to determine the degree of association between response variables.

2 Results

2.1 Diurnal gas exchange and water use efficiency It was found that *Ulmus pumila* (tree species) had significantly higher transpiration rate (E) and stomatal conductance (g_s) but lower photosynthetic rate (A) compared to the other two species during the daytime (Fig. 1a,b,c). Instantaneous water use efficiency (WUE) was significantly lower in *U. pumila* (tree) than in *S. gordejevii* (shrub) and *L. chinensis* (herb) (Fig. 1d). Considering the whole days gas exchange patterns, *S. gordejevii* and *L. chinensis* showed distinct two peaks in both A and E as well as g_s, appearing at 8:00 or 10:00 and 16:00, respectively. While *U. pumila* had only one peak appearing at 10:00, after which all the values decreased till the night.

2.2 Correlations amongst gas exchange variables Significantly positive correlations were noted between g_s and A or E for all the species measured (Fig. 2). The multiple species data pool also showed that trees had lower A (Fig. 2a) and higher E (Fig. 2b) than shrubs and herbs at the same stoma aperture. Tree species assimilated less CO_2 per unit g_s than shrubs and herbs, as indicated by the lower slope of A vs g_s in trees (Table 1). However, the slope of E-g_s in trees was significantly greater than in shrubs and herbs ($p<0.05$).

All the species from different PFTs showed positively correlation between E and A ($p<0.05$). At the same E values, however, tree species had the lowest A whereas shrubs and herbs had the similar higher values (Fig. 3). The slope of A versus E (means WUE) in all the three PFTs was in the order: trees <herbs<shrubs (Table 1). The results indicate that per change of E lead to the lower A changes in trees than in shrubs and grasses, which reflected the lowest water use efficiency in trees.

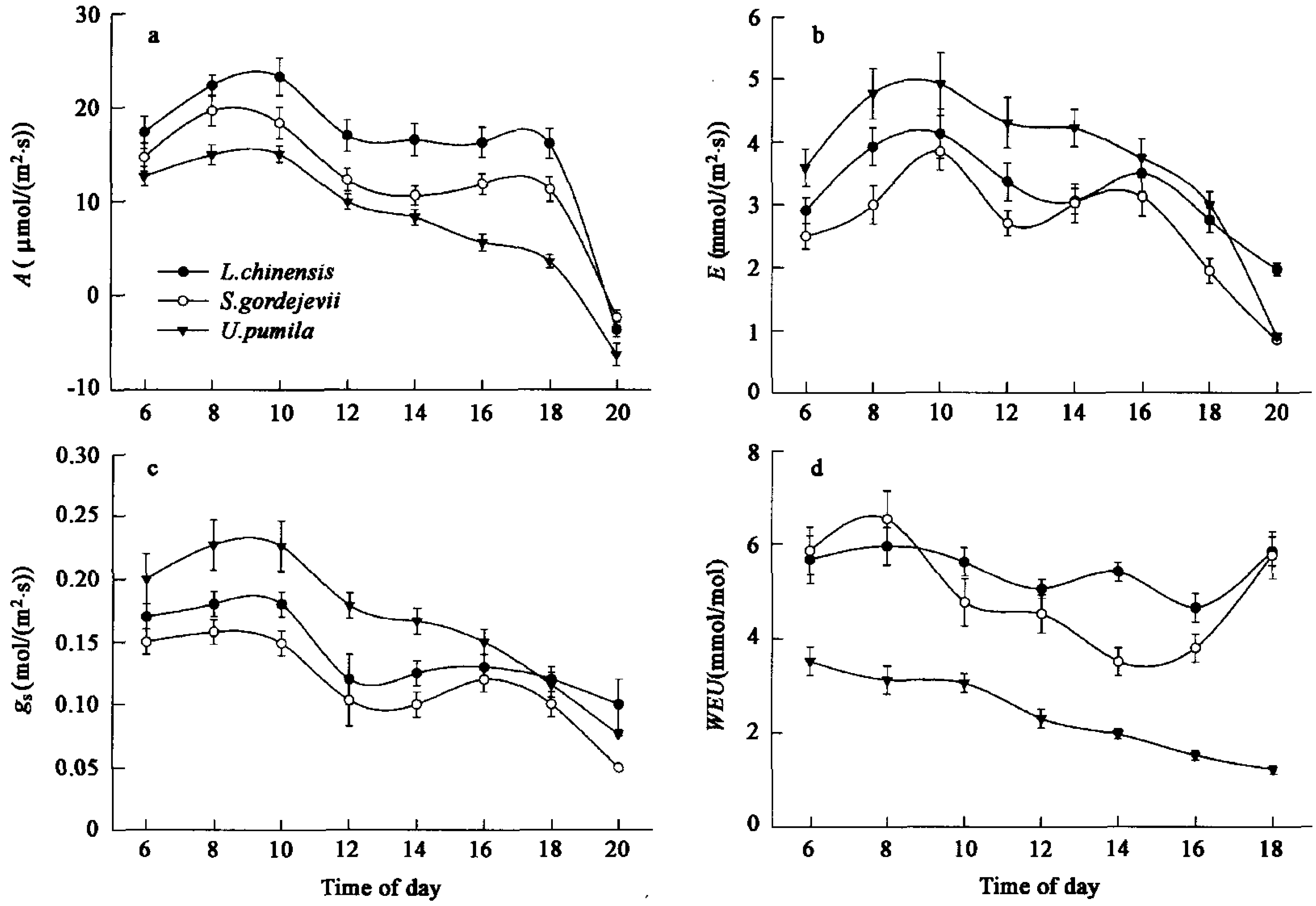

Fig. 1 Diurnal patterns of gas exchange in three plant functional types measured on 5 and 6 July, 2002 in Hunshandak sandland

a photosynthetic rate (A); b transpiration rate (E); c stomatal conductance (g_s); d water use efficiency (WUE); Error bars are ± SE

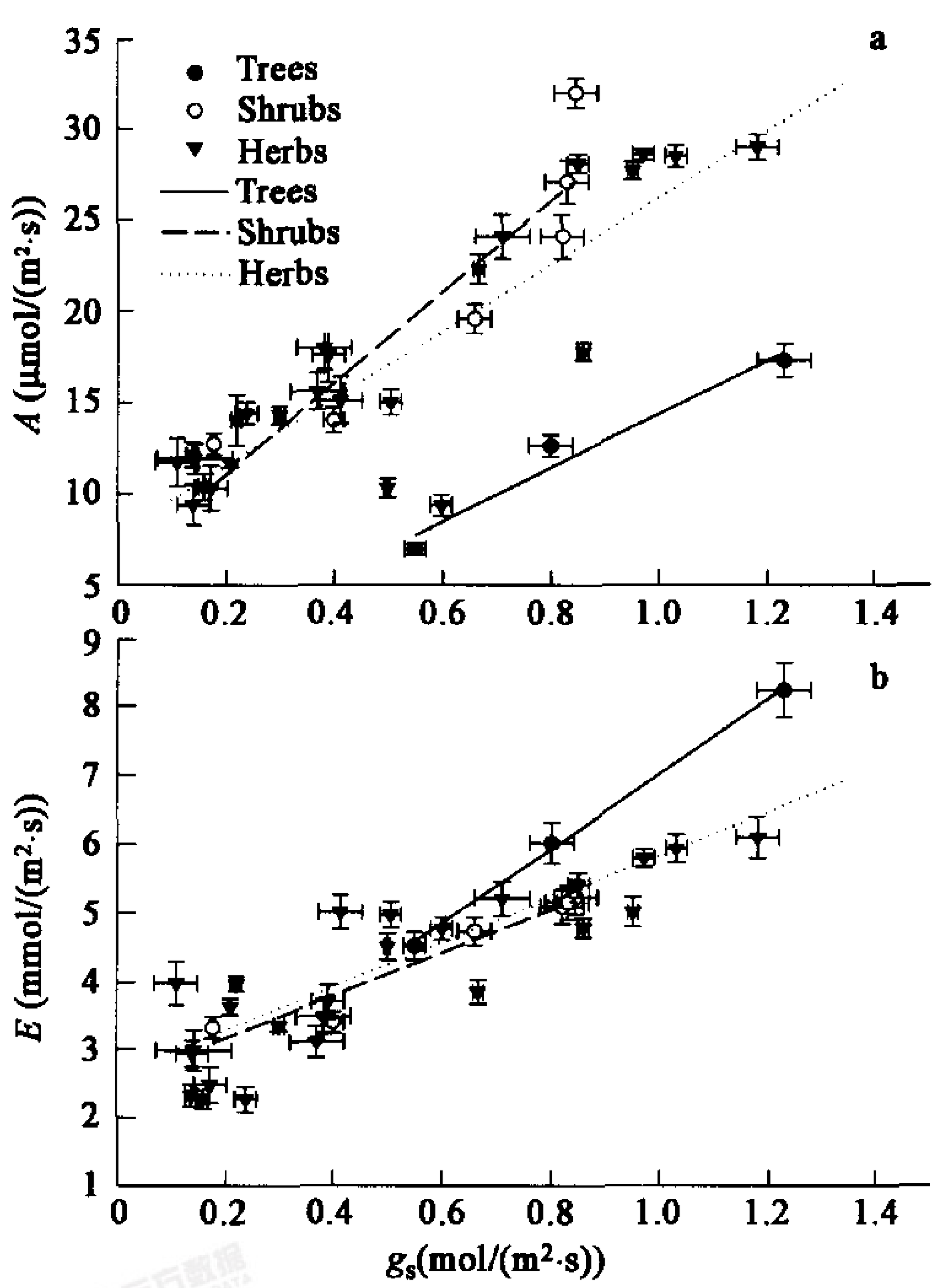

Fig. 2 Relationships between g_s and A (a) or E (b) for three PFTs in Hunshandak sandland

Regression lines are shown separately for each PFTs; Error bars are ± SE

Table 1 Relationships amongst variables in three PFTs

Variables	PFTs	n	Slope	r^2	p
	trees	9	14.713	0.959	0.022
A-g_s	shrubs	18	25.051	0.835	0.005
	grasses	75	18.42	0.656	0.001
	trees	9	5.45	0.998	0.001
E-g_s	shrubs	18	3.118	0.944	0.001
	grasses	75	3.19	0.6	0.001
	trees	9	2.718	0.974	0.002
A-E	shrubs	18	7.892	0.853	0.004
	grasses	75	3.415	0.382	0.001
	trees	9	0.7	0.975	0.002
g_s-Ψ_{leaf}	shrubs	18	0.247	0.97	0.001
	grasses	75	0.253	0.538	0.001

Sample size (n), coefficient of determination (r^2), slopes of relations and level of significance (p)

2.3 Stomatal conductance versus leaf water potential

Across the 34 species from different PFTs, stomatal conductance enhanced with the increasing leaf water potential (Ψ_{leaf}) (Fig. 4). However, trees changed their g_s much larger than shrubs and herbs per unit change of Ψ_{leaf} (Table 1), as reflected by the larger slope of tree in g_s vs Ψ_{leaf}. At the same Ψ_{leaf}, trees had the highest g_s values among the three PFTs.

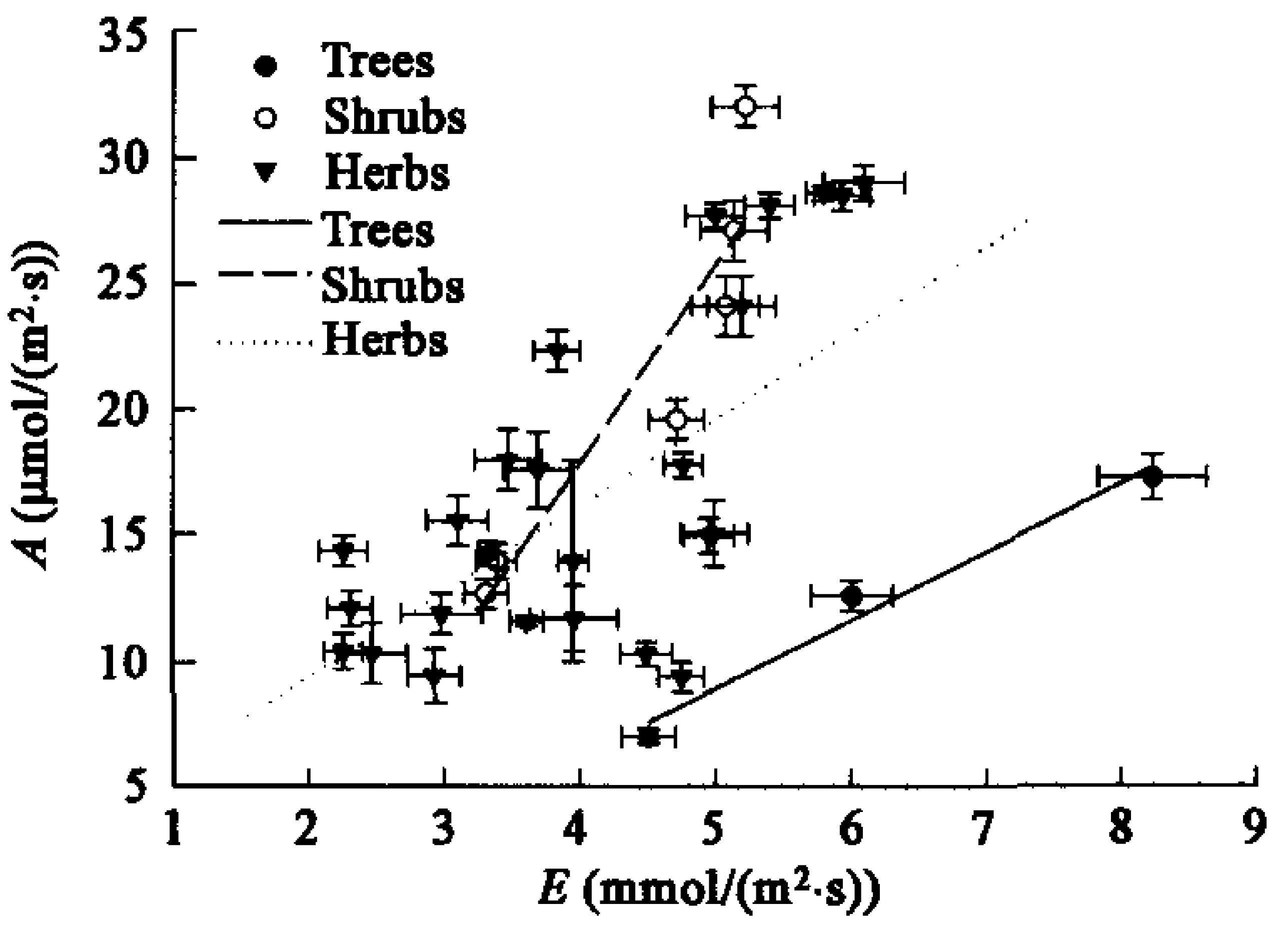

Fig. 3　Relationships between E and A for three PFTs in Hunshandak sandland

Regression lines were shown separately for each PFTs; Error bars are ± SE

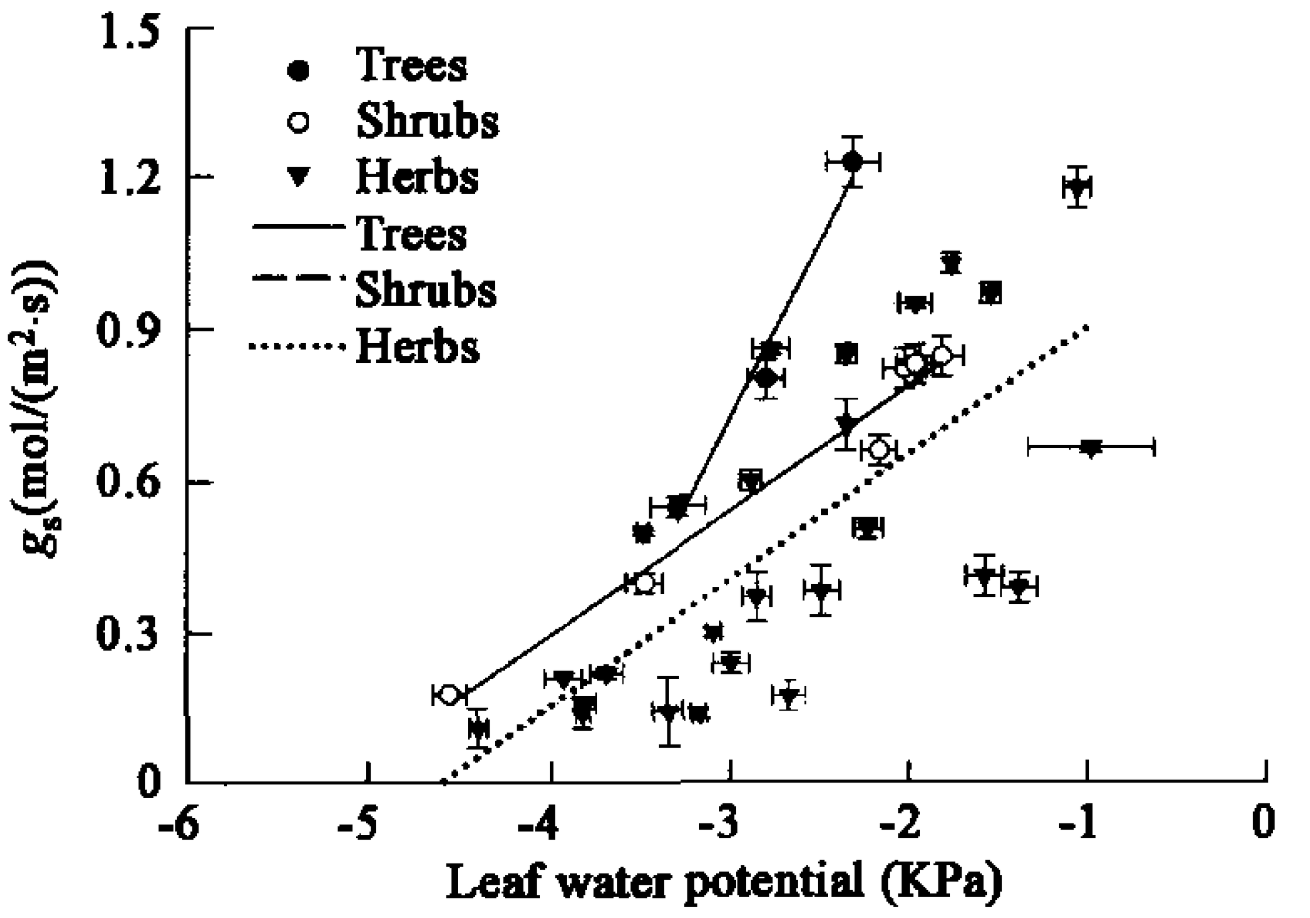

Fig. 4　Relationships between Ψ_{leaf} and g_s for three PFTs in Hunshandak sandland

Regression lines were shown separately for each PFTs; Error bars are ± SE

3　Discussions

Stomata controls the carbon-water balance in plants by acting as transport for diffusive CO_2 uptake and water vapor loss[27]. Drought-resistant species should have strong stomata control over gas exchange, *i.e.*, stomata maximize the rate of carbon gain while minimizing water loss. Instantaneous control of transpiration flux by stomata often represents an additional constraint to plant productivity. Therefore, poor stomatal control in plants, with leaves continuing to lose water under severe water deficit is inefficient water use types. In our study, tree species use water less efficiently than shrubs and grasses, which were reflected as follows.

The larger slope of E vs g_s($\Delta E/\Delta g_s$) in trees (Table 1) indicating more water was transpired per unit g_s than grasses and shrubs. Contrary to the changes of E, A in trees showed the least slope versus g_s among the different PFTs (Fig. 2a), indicating the lower photosynthetic capacity for the same stomatal aperture. In fact, transpiration in trees with the same stomata aperture was somewhat higher, and photosynthetic rate was lower than in grasses and shrubs (Fig. 2b). So, we could infer that trees assimilate carbon at the expense of transpiring more water than shrubs and herbs, i. e., trees using water inefficiently.

In theory, optimal A/E is a function of a balance between maximum uptake of ambient CO_2 and minimal E, which might be regulated primarily by g_s[28]. The lower photosynthetic capacity and larger transpiration rate made less *WUE* in trees (Fig. 1d), which could also be illustrated by the lower $\Delta A/\Delta E$ (slope of E vs A) (table 1). The difference among species or PFTs in the response of A and E to g_s reflects the inefficient water use strategy in trees.

In addition, trees showed less ability to regulate stomata. For the diurnal gas exchange changes, trees showed one-peak pattern in A, E and g_s during the daytime (Fig. 1). At the midday time, when high photosynthetic photo flux density (PPFD) (>2000 μmol/(m² · s)) and high temperature (>38℃) appeared, trees closed their stomata and could not resumed at the favorable conditions in the afternoon. While shrubs and herbs transitorily closed their g_s to prevent higher transpiration at midday time but reopened stomata when temperature and PPFD was appropriate in the afternoon. This reflects the less flexibility of stomata in trees.

Water potential is assumed to be a measure of plant water status, which is related to soil water availability and plant hydraulic conductivity[29]. A positive correlation between g_s and leaf water potential was established for each PFTs (Fig. 4). However, trees behaves as a life-form very sensitive to low water potential, because it changed g_s much more than other two types per unit Ψ_{leaf} (Fig. 4), which means that trees were more sensitive to drought compared with herbs and shrubs.

From the above analysis, we could conclude that trees had lower water use efficiency and more sensitive to drought. Previous study also declared that trees consumed more water than herbs when the water moisture is deficit[30]. Arid and semiarid regions are not only lack of rainfall but also very fluactuated in the intensity, frequency and seasonal distribution of rainfall[31, 32]. So, drought might happen incidentally in these regions, which became a threat to survival for the plant species, especially trees being most sensitive to moisture changes in an arid ecosystem. Taken our results into account, we recommend using shrubs, such as *Salix matsudana* Koidz, *Salix gordejevii* L., and herbs, such as *Leymus chinensis* and *Agriophyllum squarrosum*, to restore the degraded Hunshandak Sandland rater than planting trees.

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